CALAMAGROSTIS TACOMENSIS (POACEAE): A NEW SPECIES FROM WASHINGTON AND OREGON

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ABSTRACT

We used PCA of morphological characters to confirm the presence of an undescribed *Calamagrostis* species in Washington and Oregon that has historically been attributed to *Calamagrostis vaseyi*. We propose to name this grass *Calamagrostis tacomensis*. It is most similar to *C. foliosa* although it has often been confused with *C. purpurascens* and *C. sesquiflora* all of which have similar lemma awn characteristics (i.e., the awn relatively long, exserted, and bent). *Calamagrostis tacomensis* has been collected at high elevations (490–2170 m) in the Washington Cascades, the Olympic Peninsula and the Steens Mountains of Oregon. The name *C. vaseyi* has been misapplied to our new species. The description of *C. vaseyi* is similar to *C. rubescens*. We have studied the specimen that has been attributed to be the type of *C. vaseyi* and it is *C. purpurascens*. We lectotypify *C. vaseyi*.

Key Words: Calamagrostis tacomensis, Calamagrostis vaseyi, Poaceae, morphology, Washington, Oregon.

In preparing the treatment of Calamagrostis (Poaceae) for the Flora of North America, we noticed several specimens from the mountains of Washington and Oregon with long, exserted, and bent lemma awns that did not match descriptions of other northwestern North American species with similar awn characteristics such as: C. sesquiflora (Trin.) Kawano, C. purpurascens R. Br., C. howellii Vasey, and C. foliosa Kearney. Most such specimens had been identified initially, or annotated later as C. sesquiflora, but did not originate from habitats and geographic locations typical of C. sesquiflora, a plant of strictly maritime/coastal environments (Marr et al. in press). Some of these specimens had also been labelled at some point as "C. vaseyi Beal" leading us to reconsider the validity of this entity. We present morphometric data from herbarium specimens to support the recognition of this Calamagrostis entity (viz. "C. vaseyi") as a distinct species, and provide a botanical diagnosis, description and comparison to other related species. We propose the new name, C. tacomensis K. L. Marr & R. J. Hebda. We also designate a lectotype for C. vaseyi and show that the morphology of this specimen falls within the range of C. purpurascens.

MATERIALS AND METHODS

In our study, we included northwestern North American species whose floral morphology was similar to "*C. vaseyi*" in having long (greater than 4.5 mm), exserted, and bent lemma awns

and often an open inflorescence (i.e., C. purpurascens, C. sesquiflora, C. howellii, and C. foliosa). Herbarium material (including five specimens of Russian C. sesquiflora) was borrowed from CAN, DAO, GH, JEPS, MO, NY, OSU, WTU, UBC, UC, US, and V, and collections at Olympic National Park and Pacific Lutheran University (Appendix 1). For 93 specimens, we measured or observed 20 leaf, inflorescence, and growth habit characters (Table 1). These data were used in the morphometric analyses and to develop species descriptions. In the descriptions, additional measurements were added in cases where those included in the morphometric analyses did not capture the full range of variation (e.g., leaf blade lengths and widths were based upon the widest, narrowest, longest, and shortest blades of the specimen regardless of position on the stem). For all specimens, we recorded information concerning habitat and collection locations.

To help establish whether or not the apparent entity is distinct from the taxa that it resembles, we applied principal components analysis (PCA) using SYSTAT (1997) in which we included the characters indicated in Table 1.

RESULTS

A non-statistical comparison of 21 characters suggests that several of them may be useful to distinguish among these species (Fig. 1). For example, *C. purpurascens* is the only species with densely tomentose upper leaf blade surfaces; inflorescence width of *C. howellii* (5.0–15.0 cm)

TABLE 1. CHARACTERS MEASURED ON SPECIMENS OF CALAMAGROSTIS FOLIOSA, C. HOWELLII, C. PURPURASCENS, C. TACOMENSIS, AND C. SESQUIFLORA. (+ designates characters used in PCA.)

Code	Explanation
Inflorescence	
+INFL +INFW	length (cm)
+BRL	width at widest point, usually the inflorescence base (cm) longest branch from the most basal inflorescence node (mm)
Spikelet	
+GL +LML GVERSUSL +GSR	first glume length (mm) lemma length (mm) glume length minus lemma length glume surface: 1 = glabrous; 2 = scabrous on keels only; 3 = whole surface scabrous;
HRAT AWBSRAT +AWNATT +AWNL	4 = scabrous and projections longer and bent callus hair length/lemma length distance from base of lemma to point of attachment of awn/lemma length distance from base of lemma to point of attachment of awn awn length (mm)
Leaf	
+LFW +LFL +INV +ULFS	width of second leaf below inflorescence (mm) length of second leaf below inflorescence (mm) leaf blade: 1 = involute; 2 = flat upper leaf surface: 1 = glabrous; 2 = slightly scabrous; 3 = very scabrous; 4 = scabrous + slightly pilose; 5 = tomentose
+LLFS +COLLAR +LIGL	lower leaf surface: 1 = glabrous; 2 = scabrous collar: 1 = glabrous; 2 = scabrous; 3 = pilose; 4 = tomentose ligule length (mm)
Stem	
+HT +NODE	total plant height (cm) number of nodes (from the root crown to the inflorescence)

is greater than that of the other species (0.5–3.0 cm); awns of *C. foliosa* (12.0–17.0 mm) and *C. howellii* (10.0–16.0 mm) are generally longer than those in the other three species (4.5–13.0 mm). Based on this comparison, *C. tacomensis* is most similar to *C. foliosa*, differing mostly from the latter in having shorter awns, glumes, lemmas, and callus hairs. Although it was not part of our analysis, *C. tacomensis* also occurs at much higher, inland sites than *C. foliosa*.

In the first PCA, the first factor accounted for 31% of the variation with awn length (AWNL), upper leaf surface (ULFS), and longest inflorescence branch (BRL) contributing most to the variation (see Table 1 for details). The second factor accounted for 16% of the variation with plant height (HT), lower leaf surface (LLFS), and number of nodes (NODE) contributing the most. A scatterplot (Fig. 2) of the PCA scores indicated that C. purpurascens and C. sesquiflora were morphometrically distinct. There was more overlap among C. foliosa, C. howellii, and C. tacomensis, nevertheless most specimens of C. tacomensis were visibly distinct from the other species. Three of the C. sesquiflora specimens from Russia clustered together with those from North America; the other two did not. The scatterplots confirmed Scribner's (1901) statement to the effect that C. tacomensis (his C. vaseyi Beal, see below) is morphologically intermediate between *C. purpurascens* and *C. howellii*. The specimen (US-556750) that we have designated as the lectotype of *C. vaseyi* plotted well outside of the range for *C. tacomensis* and clearly together with *C. purpurascens*.

In a second PCA, we removed *C. purpurascens* and C. sesquiflora from the analysis and included the same set of characters as the first PCA. The first factor accounted for 29% of the variation with lemma length (LML), callus hair length (HARL) and glume length (GL) contributing the most. The second factor accounted for 18% of the variation with plant height (HT), leaf width (LFW) and inflorescence length (INFL) contributing the most. The third factor accounted for 12% of the variation with inflorescence width (INFW), upper leaf surface (ULFS), and inflorescence branch length (BRL) contributing the most. A scatterplot (Fig. 3) of the PCA scores indicated that there was almost no overlap among C. foliosa, C. howellii, and C. tacomensis, especially on the first axis.

DISCUSSION

Our analyses indicate that there is a group of specimens that are morphologically as well as ecologically and geographically distinct from any of the currently recognized species of *Calamagrostis*. Earlier botanists noted that these

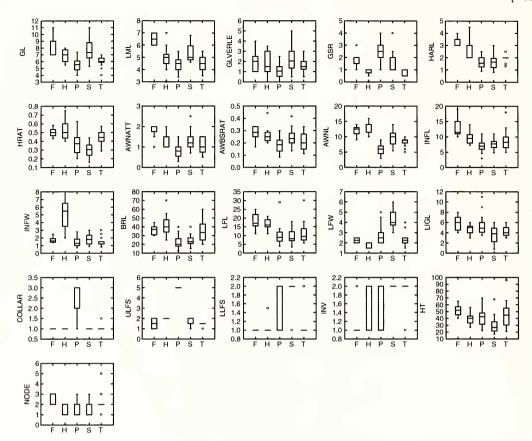


Fig. 1. Univariate plots of characters measured for *Calamagrostis* species from northwestern North Amercia having long, exserted, and bent awns. Species labelled as following: F = C. foliosa, F = C. howellii, F = C. purpurascens, F = C. sesquiflora, F = C. tacomensis. All length measurements in millimeters, except for the following that are in centimeters: INFL, INFW, LFL, and HT. Character abbreviations per Table 1.

plants are distinct from other species of *Calamagrostis*, and sometimes misapplied the name "*C. vaseyi*" to them. Furthermore, the specimen that has been regarded as the type of *C. vaseyi* belongs to *C. purpurascens*. In the following section we outline the history of *C. vaseyi* and demonstrate why the name cannot be used. We provide a name, *C. tacomensis*, for the above mentioned group of specimens and a key and descriptions for *C. tacomensis* and morphologically similar species of northwest North America.

Taxonomic and Nomenclatural History of Calamagrostis vaseyi

Calamagrostis vaseyi Beal was first published in Beal (1896). The protologue indicates that it was based on a collection made by U.S. Department of Agriculture botanist, G. R. Vasey: "Washington (Cascade Mountains), Vasey. Alaska to Washington." In the US type collection there is a specimen (US-556750), that has been considered the type specimens for C. vaseyi (Fig. 4). This specimen has been annotated by at

least three different individuals, none of whom gave their name. Beal was not one of them. One annotation is simply "Type of C. vaseyi Beal." In the handwriting of a second person are the following two statements: 1) "In Beal Herb. is a duplicate of this with labels in Vasey's script "Calamagrostis purpurascens R.Br.—the genuine plant"; and 2) "It is not named "C. vasevi"there is no Beal script in connection with this specimen". Following the first statement above, lightly in pencil is written "cf. C. purpurascens." In the handwriting of a third person are the following: "Calamagrostis rubescens ["rubescens" has been crossed out]; locality: Cascade Mts. Washington; collector G.R. Vasey 1889." Hitchcock et al. (1969) noted, and we agree, that this specimen is actually *C. purpurascens*. Beal (1896) designated a type collection for C. vaseyi but did not specify a particular sheet in a specific herbarium. To preclude future nomenclatural problems, we are designating US-556750 as the lectotype of C. vasevi, a designation that is in keeping with past practice. We have been unable to locate the specimen that is alluded to in comment 1 above.

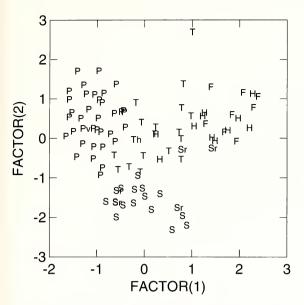
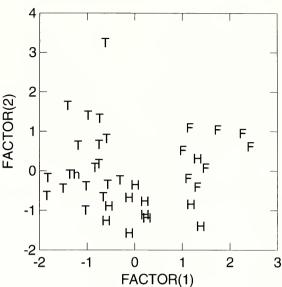


FIG. 2. Scatterplot of the first two components from a PCA of morphological characters of northwest North American *Calamagrostis* species having long, exserted, and bent awns. Species labelled as following: F = C. foliosa, H = C. howellii, P = C. purpurascens, S = C. sesquiflora, S = C. sesquiflora collected from Russia, S = C. tacomensis, S = C. vaseyi lectotype, S = C. tacomensis holotype.

Calamagrostis vaseyi Beal—LECTOTYPE HERE DESIGNATED: U.S.A: "Cascade Mts. Washington", 1889 G.R. Vasey s.n. (Lectotype: US 556750).

Beal's description for C. vasevi matches that of C. rubescens Buckley in the following characters: leaf length and width, the presence of hairs at the leaf collar, glume length, awn length and position of attachment to the lemma, and callus hair length. He described the awn as straight, whereas it is bent in C. rubescens. Scribner (1901) recognized C. vasevi Beal, and provided an illustration in his own hand (we do not know what specimens he viewed) and noted that C. vaseyi is "intermediate between C. purpurascens and C. howellii." However, neither Scribner's description, nor his illustration, matches the description given by Beal (1896). Under synonymy, Scribner stated: "C. purpurascens of Vasey, Contr. U.S. Nat. Herb. 3:82, 1892. Not R. Br. 1823." Vasey (1892), under C. purpurascens states the following: "This description is from specimens collected in the Cascade Mountains of Washington by G. R. Vasey, which agrees well with European specimens, although differing somewhat from the description in Hooker's Fl. Bri. Am. It occurs also in British America and in Sitka." From these comments it is evident that Vasey perceived that the entity he collected in



1889, and described as *C. purpurascens*, did not entirely match *C. purpurascens* R. Br.

Calamagrostis vaseyi was recognized as distinct from *C. purpurascens* in several early regional floras of British Columbia (Henry 1915) and the Pacific Northwest (Howell 1897; Piper 1906; Frye and Rigg 1912; Abrams 1923; Jones 1938). The descriptions by these authors differ somewhat from each other and most seem to fit *C. purpurascens*. Only Piper (1906) cites specimens he actually viewed, from the following locations: Olympic Mountains, Mount Rainier, Goat Mountains, and Skamania County. Piper and Beattie (1915) listed *C. vaseyi* but not *C. purpurascens*. Hitchcock (1951) listed *C. vaseyi* under *C. purpurascens*.

Calamagrostis vaseyi has also been confused with C. sesquiflora. Kawano (1965) in his treatment of the "C. purpurascens complex" viewed ten Washington state specimens and concluded that they belonged to C. sesquiflora. It appears that this was the first application of the name C. sesquiflora to plants from Washington State. Hitchcock et al. (1969) followed Kawano (1965) and reported that C. sesquiflora occurred "On cliffs and shaded to open rocky montane to subalpine slopes in our area, mostly at elevations of 3500–6000 ft.; Olympic Mts., and the Cascade and Wenatchee Mts., Wash., from Kittitas Co. to Skamania Co.; Aleutian Is. to n.e. Asia."

We have viewed most of the specimens from Washington that Kawano annotated as *C. sesquiflora*; all fit the concept and criteria of

Fig. 4. Label of the specimen that we designate as the lectotype for Calamagrostis vaseyi (US 556750).

what we propose to call *C. tacomensis* (Fig. 5), a previously overlooked species that is distinct from both *C. purpurascens* and *C. sesquiflora* (Figs. 2, 3). These specimens bore earlier labels identifying them as either *Trisetum sesquiflorum* Trin., *Deyeuxia sylvatica* Kunth var. *americana* Vasey, *C. purpurascens* R. Br. or *C. vaseyi* Beal. Further confusion resulted because some specimens that are actually *Trisetum spicatum* (L.) Richt., have been annotated as *Calamagrostis sesquiflora* arising from the earlier inclusion of the species in *Trisetum*.

Typification of Calamagrostis tacomensis

"Tacoma" is a Native American name for Mt. Rainier near Seattle; because many collections of this species come from that mountain, we chose it for the specific epithet. To our knowledge, the specimen that we have chosen for the type is the earliest collection made.

Calamagrostis tacomensis K. L. Marr and R. J. Hebda, sp. nov.—TYPE: U.S.A. Washington: Skamania County, rocky mountain-sides, 11 Aug. 1886, W.N. Suksdorf 909 (Haplotype: MO-1772987!; Isotype: NY!)

A Calamagrostis foliosa similaris, sed glumis, lemmae, aristae et pilis calli brevioribus.

Plants without sterile culms; cespitose, sometimes densely so, usually without rhizomes, if present, rhizomes short (about 2 cm) and stout (2-3 mm thick). Culms (20)30-55(95) cm, unbranched, smooth or slightly scabrous beneath the panicles; nodes (1)2(5). Sheaths and collars smooth to slightly scabrous; ligules (3)3.5-5.5 (6) mm, mostly entire and truncate to obtuse, sometimes lacerate; blades (6)7–14(30) cm long, (1.5)2-2.5(4) mm wide, flat, abaxial surface smooth or rarely slightly scabrous, adaxial surface usually slightly scabrous, rarely smooth. Panicles (5)7-10(18) cm long, (0.5)1-2(3) cm wide, loosely contracted, sometimes open, erect to slightly nodding, shiny green and purple; branches (2)2.3–4(6) cm long, scabrous, with spikelets mostly on the distal 2/3, sometimes to the base. Spikelets (4)6-6.5(7) mm, often green with a purple patch at the base; rachilla prolongations 1.5-2(2.5) mm, with (1.5)2(3) mm hairs. Glumes keeled, sparsely scabrous on the keel towards the glume apices, lateral veins mostly prominent, apices acute to short acuminate, tips not twisted; callus hairs (1.2)2(2.5) mm, (0.3)0.4-0.5(0.6) times as long as the lemmas, abundant; lemmas (3.5)4–5(5.5) mm, (0.5)1.5– 2(3) mm shorter than the glumes; awns (5.5)7– 8.5(10) mm, attached to the lower 1/10-1/3 of the lemmas, exserted (greater than 2 mm), easily distinguished from the callus hairs, strongly bent; anthers (1)2-3(3.5) mm. 2n = unknown.



FIG. 5. Illustration of *C. tacomensis*.

Comments. The type specimen of C. tacomensis was originally labelled as Deyeuxia sylvatica, Kunth, var. (Deyeuxia is a genus sometimes combined with Calamagrostis.) The holotype has been annotated as C. vaseyi Beal. At US is a third specimen that we have seen whose label bears the following: "Deyeuxia. Dry rocks on high mountains 11 Aug. 1886, Suksdorf 201." The epithet sylvatica was added later in a different handwriting; a third person later annotated it as C. vaseyi Beal. Because the US specimen bears a different collection number, we have not included it as an isotype, although it was evidently collected from the same location and on the same date.

Calamagrostis tacomensis is currently known only from three regions: Cascade Mountains of Washington, the Olympic Peninsula of Washington, and the Steens Mountains of southeast Oregon. The Steens Mountains specimens are somewhat more robust than those of Washington State. Clarification of the taxonomy of this and the other morphologically similar species removes C. sesquiflora from the flora of Washington State.

Ecology of Calamagrostis tacomensis

Calamagrostis tacomensis grows in mountains, mostly in open, moist to dry sites from 490–2170 m. Notable on many of the herbarium labels are the words "rock", "rocky", "crags" and "cliffs", but sandy and sandy loam soil textures are also recorded, and the species occurs from ridge top to valley bottom positions.

Compared to morphologically similar species in the region, the ecological requirements seem to be similar to but probably macroclimatically moister and milder than those of *C. purpurascens*, a species that also occupies mid to high elevations but is mostly in more continental climates. Unlike *C. tacomensis*, *C. purpurascens* is commonly associated with forested conditions in addition to the open habitats typical of *C. tacomensis*. Compared to *C. sesquiflora*, the relative macroclimatic conditions of *C. tacomensis* are more

inland and continental. Calamagrostis sesquiflora would seem in North America at least to have limited drought and cold tolerance, growing predominantly in sites within a few kilometres of the open ocean or at sites under strong maritime influence from sea-level to 1100 m. Although it occurs on rocky sites, these are almost always moist and soils with abundant organic matter (bogs, heaths) are often noted.

Like Calamagrostis tacomensis, C. foliosa and C. howellii have a limited geographic distribution and a preference for rocky sites and cliffs. Both, however, are lower elevation species (C. foliosa from 0–1220 m and C. howellii from 100–450 m) suggesting limited or no tolerance of significant frost, particularly C. foliosa. Of all the morphologically similar species, C. howellii grows in the most similar habitats and nearest to C. tacomensis, but at lower elevations and for that reason likely under drier conditions.

CONCLUSIONS

It is critical to carry out comprehensive field surveys, collections, and ecological/habitat observations of C. tacomensis, because it appears to have a limited distribution. The range may well be greater than so far recognized by us from herbarium material. A thorough investigation of the southern Cascade Mountains northward into British Columbia and the Olympic Mountains is required as well as isolated adjacent high ground. In this context, the morphological distinctness of C. tacomensis in the Steens Mountains suggests either long-distance dispersal or more likely relict populations of a species that was more widespread during cool climates of the late Pleistocene. A genetic study using DNA markers might clarify the above question as well as evaluate the relationship of C. tacomensis to the other longawned species of this region, in particular C. foliosa. It would also be useful to have a chromosome count for this species.

KEY TO SOME LONG-AWNED *CALAMAGROSTIS* SPECIES FROM BRITISH COLUMBIA, WASHINGTON, OREGON AND CALIFORNIA

Calamagrostis foliosa. Plants sometimes with sterile culms; cespitose, short (less than 1 cm) rhizomes rarely present. Culms (25)30–60(70) cm, unbranched, sparsely scabrous beneath the panicles; nodes 1-3. Sheaths and collars usually smooth; ligules (3)4–6(7) mm, mostly entire and truncate to obtuse, sometimes lacerate; blades (10)11-21(27) cm long, (1.5)2-2.5(4) mm wide, mostly basal, flat or involute, abaxial surface smooth, adaxial surface slightly scabrous. Panicles (9)10-12(19) cm long, 1-1.5(2.5) cm wide, erect to slightly nodding, contracted, branches sometimes slightly spreading at the base, usually pale green, rarely pale purple; branches (2)3-4(5) cm, sparsely scabrous, with spikelets to the base. Spikelets (7)8–11 mm; rachilla prolongations (1.5)2–(3) mm, prominently bearded, hairs to 2–3 mm. Glumes keeled, smooth or scabrous on the keel, lateral veins prominent, apices acuminate; callus hairs 2.5-3(4) mm, 0.4-0.6 times as long as the lemmas, abundant; lemmas (5)6-7(8) mm, (0.5)1-2(3) mm shorter than the glumes; awns 12–14(17) mm, attached to the lower 1/5-2/5 of the lemmas, exserted (greater than 2 mm), easily distinguished from the callus hairs, bent; anthers 3-4.5 mm. 2n = 28.

Calamagrostis howellii. Plants sometimes with sterile culms; densely cespitose, rhizomes rare, if present, less than 1 cm. Culms (25)35–45(60) cm, unbranched, smooth or slightly scabrous beneath the panicles; nodes 1–2. Sheaths and collars smooth; ligules (2.5)3.5–6 mm, lacerate, if not too torn then acute; blades (9)12–20(25) cm long, 1-2.5(3) mm wide, flat to involute, abaxial surface smooth, adaxial surface finely scabrous. Panicles (5)7–12(15) cm long, (2)3.5–6.5(8) cm wide, loose and open, straw-colored, green to purplish; branches (2)3.5–5(7) cm, smooth or sparsely scabrous, with spikelets often, but not always, concentrated in the distal 1/2 of the branchlets. Spikelets (5.5)6–8 mm; rachilla prolongations 1-1.5(2) mm, with (1.5)2-2.5(3) mm hairs. Glumes rounded to slightly keeled, smooth or scabrous only on the apices, lateral veins usually prominent and raised, apices acuminate; callus hairs 2-3(4.5) mm, 0.4-0.6(0.7) times as long as the lemmas, abundant; lemmas 4.5-5 mm, about 2 mm shorter than the glumes; awns (10)13–16 mm, attached to the lower 1/5– 2/5 of the lemmas, exserted, stout, easily distinguished from the callus hairs, strongly bent; anthers (2)2.5-3(4) mm. 2n = 28.

Calamagrostis purpurascens. Plants apparently without sterile culms; strongly cespitose, often with short (1–4 cm), moderately stout (1–2 mm thick) rhizomes. Culms (10)30–80 cm, usually unbranched, occasionally branched, slightly to strongly scabrous, sometimes short hairy beneath the panicles; nodes (1)2(3). Sheaths scabrous; collars mostly scabrous to hairy, rarely smooth;

ligules (1.5)2–4(9) mm, usually entire and truncate, sometimes lacerate. Blades (4)5–17(30) cm long, 2–5(6) mm wide, flat or involute, stiff. abaxial surfaces scabrous, adaxial surfaces densely long hairy, rarely sparsely hairy. Panicles 4-13(15) cm long, 0.9-2(2.8) cm wide, erect, contracted, infrequently interrupted near the base, often red- or purple-tinged; branches 1.3-3.5 cm, scabrous, with the projections long, almost hairy, and with spikelets to the base. Spikelets (4.5)5.5–6.5(8) mm, with 1(2) florets: rachilla prolongations about (1)2 mm, with about 2 mm hairs. Glumes keeled, commonly scabrous on the entire surface, rarely scabrous on the keel only, lateral veins obscure to prominent, apices acute; callus hairs (0.9)1.2-1.5(2.4) mm, 0.2-0.4(0.6) times as long as the lemmas, sparse; lemmas (3.5)4-4.5(5) mm, 1-2.5 mm shorter than (rarely equal to) the glumes; awns (4.5)6-7(9) mm, attached to the lower 1/10–1/3 of the lemmas, exserted (except rarely when the awn is 4.5–5 mm long), stout, easily distinguished from the callus hairs, bent; anthers (1.3)1.7– 2.5(2.9) mm. 2n = 42-58, 84.

Calamagrostis sesquiflora. Plants rarely with sterile culms; strongly cespitose, usually without rhizomes or with short (1–2 cm), moderately stout (1–2 mm thick) rhizomes. Culms (15)30– 46(50) cm, unbranched, usually smooth, rarely slightly scabrous beneath the panicles; nodes 1-2(3). Sheaths and collars smooth; ligules (0.5)2– 5(6) mm, entire and mostly truncate (obtuse) to lacerate; blades (3)8-25(31) cm long, (2)3-7 mm wide, flat, abaxial surface scabrous, rarely smooth, adaxial surface smooth or slightly scabrous. Panicles 4-11(12) cm long, 0.8-2.5(2.8) cm wide, erect, contracted to somewhat open, usually purple-tinged, sometimes brown or green; branches 1.5–3(4) cm, scabrous, with the projections sometimes long, almost hairy, and with spikelets to the base, except sometimes on the lowest branches. Spikelets (5)5.5-8.5(9.5) mm; rachilla prolongations (1)1.5(2.2) mm, with 1-2.2 mm hairs. Glumes keeled, scabrous, usually for the full length of the keel and sometimes on the entire surface, lateral veins prominent, apices long-acuminate, tips often twisted; callus hairs (0.8)1.2–1.8(3) mm, 0.1–0.4 times as long as the lemmas, abundant; lemmas (3.5)4-4.5(6) mm, (0.5)1-2.5(4.5) mm shorter than the glumes; awns (5.4)7-11(13) mm, attached to the lower 1/10-2/5 of the lemmas, exserted (greater than 2 mm), stout and easily distinguished from the callus hairs, bent; anthers (1.2)2.2-3(3.4) mm. 2n = 28.

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Appendix I

Specimens Examined

* = specimen included in morphometric study; (Herbarium abbreviations are according to acronym except for the following: Luth. = Pacific Lutheran

except for the following: Luth. = Pacific Lutheran University; Olym = Olympic National Park Herbarium)

Calamagrostis foliosa: USA, California: Del Norte Co.: Red Mountain, E of Klamath Glen; Six Rivers National forest, 4000 ft, 7 July 1964, Van Deventer 1054-B, (JEPS); Humboldt Co.: Hardy Creek, May-1900, Joseph Burtt Dav, 6602 (UC); Mattole river at bridge 3 miles E of Petrolia, 100 ft, 9 June 1936, *Tracy* 14899* (OSU,UC); near "Panther Gap" on road between Mattole and Bull Creek, 2700 ft, 17 June 1938, Tracy 15967A*,15967B* (UC), 145052; Shelter Cove, mouth of Telegraph Creek, 13-Sep-1986, Berg s.n. (UC); mouth of Hardy Creek, May 1900, Davy, s.n.*, (GH); Mendocino Co.: 31 July 02, Congdon s.n.* (GH); Bridal Veil, 24 June 1911, Peck 994 (OSU); Hoerlein's, along Hood River, 45°43'N, 121°32'W, 14 June 1924, Henderson 1023 (GH, OSU); Oneanta tunnel, Columbia River Gorge, 12 June 1928, Thompson, 4705, (WTU); Calamagrostis howellii: USA, Oregon: Multnomah Co.: John Yeon State Park, by McCord Creek, along Columbia R. Highway, 28-Sep-1980, Chambers 4746 (OSU); Lataurelle Falls, 3 July 1935, Thompson, 11842, (WTU); Multnomah Falls, 2 July 1965, Hitchcock 23746 (WTU); McCord Cr., near Warrendale, Columbia River Gorge, May-1972, Jaques s.n. (OSU); Columbia R. gorge, on Tanner Creek, near the falls 1 miles. of Hwy. 80N; R7E, T2N, NE1/4 of Sect. 33, 320 ft., 29 Aug. 1976, Kemp, s.n.* (OSU); JONES, N. J. 1938. The flowering plants and ferns of Mount Rainier. The University of Washington, Seattle, WA.

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Hood River Co.: Canyon of Eagle Cr., 30 May 1927, Peck 14924* (OSU); at Latourell falls, 2 July 1965, Hitchcock 23740* (OSU); Multnomah Falls, 14 Jun 1903 Sheldon S.12110 (OSU); Cliffs of Columbia River near the Cascades, May 1881, Howell s.n. (WTU); Hood R., May 1891 (OSU); Sandy R., 9 July 1883, Henderson s.n. (OSU); Rooster Rock, July 1889, Gorman s.n. (WTU); Washington: Skamania Co.: Cooks, 45°43′N, 121°40′W, 9 July 1909, Suksdorf s.n. (GH); Cooks, 9 July 1909, Suksdorf s.n.* (WTU); along the Columbia R. in drier areas of cliffs at Cape Horn; at e. end of railroad tunnel, 8 July 1966, R.&M. Spellenberg & Sutherland 1189* (OSU,WTU,UBC); Prindle, 26 May 1924, Suksdorf 11696 (WTU).

Calamagrostis purpurascens: CANADA, British Columbia, Cheslatta, Cariboo-Chilcotin, Kritchlow property; 1 kilometre E of Cheslatta, 53°48′36″N, 125°47′12″W, 12 July 01, Hebda & Fitton 01-19119*, (V); Robb Lake, Peace River, slopes on N side of lake, 56°54'N, 123°48'W, 1524 m, 30 July 1977, Argus & Haber, 10303* (V); Fern Lake, Peace River, near and around outlet E end of the lake, 57°45'N, 124°47'W, 1371.6 m, 5 Aug. 1977, Argus & Haber 10642* (V); Wokkpash Lake, Liard River Basin, slopes-W of the NW end of the lake; S of the creek, 58°27′N, 124°53′W, 1280.16 m, 19 July 1977, Argus & Haber 10729* (V); Gladys Lake, Stikine River, SE face of Ptarmigan Ridge, 57°35′N, 128°47′W, 1280 m, 16 July 1975, Pojar 107f* (V); Mt. Stephen, Yoho National Park, at Field, 49°50′N, 115°34′W, 2133 m, 19 Aug. 1953, Calder & Savile 12070* (DAO); Pope, Mount, Cariboo, a few miles NW of Fort St. James, 54°30'N, 124°20'W, 1472 m, 31 July 1954, Calder, Savile & Ferguson 13817* (V); Flathead area; Inverted Ridge, Kootenay, S Peak and saddle N of it, 49°07'N, 114°45'W, 31 July 1983, Ogilvie & Ceska, 15902* (V); Begbie, Mount, Cariboo,

51°29′N, 121°22′W, 23 June 1944, Eastham 17026* (V); Sinkut Mountain, Cariboo-Chilcotin, near Vanderhoof, 53°49′N, 123°58′W, 1463m, 18 July 1945, Eastham 18828*, (V); Skagit River, Lower Fraser Valley, Unnamed mountain 2217 m total height S of Finlayson Peak in Skagit Drainage, 49°05'N, 121°13'05"W, 2150 m, 12 Aug. 1988, Ceska, & Ogilvie 24997* (V); Skookumchuck, Kootenay, 0.1 mile up Regional Garbage Dump Road, 49°44'N, 115°43'W, 750 m, 2 July 1976, Ferster 76-1978* (V); Taseko River, Cariboo-Chilcotin, valley side on E by Taseko River Road, 51°36'N, 123°42'W, 1370 m, 14 July 1978, Pavlick & Sax 78-19571* (V); Tanzilla River, 2 kilometres above junction with Stikine River, 58°03'N, 130°54'W, 650 m, 10 July 1980, A.&O. Ceska & Polster 8054* (V); Hutchison Lake, 59°47′30″N, 126°40′W, 760 m, 21 Aug. 1979, A.&O. Ceska, Polster, & Martens 8061* (V); Buckley Creek, above Klastline River, 58°56′N, 130°46′W, 600 m, 29 Aug. 1979, A.&O. Ceska & Polster 8073* (V); Upper Dean River Road, 52°33'N, 125°19′30″W, 1100 m, Harcombe AH-1979-1930* (V); Flathead, Kootenay, ca. 5 mi. from Canada-US border, 49°08'N, 114°35'W, 2042 m, Jul-1973, Dick FR24* (V); Liard Hot Springs Park, Liard River, 59°25'N, 126°06′W, 430 m, 10 July 1971, Brayshaw & Barrett s. n.* (V); Mount Ole, Liard River, Liard Hot Springs Provincial Park, 59°25'N, 126°03'W, 760 m, 7 July 1971. Brayshaw & Barrett s. n. * (V): Tuva River, Stikine District, breaks of the river, 5 miles above crossing, 58°08'N, 130°44'W, 610 m, 8 Aug. 1971, Brayshaw & Barrett s.n.* (V); Lillooet, Headwaters of Blue Creek, 51°02′N, 122°28′W, 1430 m, 13 July 1987, Ceska, Ceska, Britton, & Anderson s.n.* (V); Cassiar, Cassiar District, 59°15'N, 129°45'W, 1000 m, 18 June 1956, Taylor, Szczawinski & Bell 391* (V); Telegraph Creek, Stikine River, slopes above Day's Ranch, 58°02'N, 130°53'W, 10 June 1980, A.&O. Ceska & Polster 4070* (V); Lower Porcupine Valley, Kootenay, Yoho National Park, 51°30′ N, 116°30′W, 1250 m, 11 Aug. 1974, Kuchar 4077* (V); Alberta, Mt. Edith Cavell, Jasper National Park, 52°40′N, 118°03′W, 28 Aug. 1964, Calder, J. A, 37200*, (DAO); Lake Edith, Jasper National Park, YMCA Lodge, 52°55'N, 118°02'W, 4 July 1955, Jenkins 5817* (DAO); Ontario, Thunder Bay, Sibley Peninsula, Thunder Cape, at the knees of Sleeping Giant, 48°18′N, 085°60′W, 24 Aug. 1957, Garton 4398* (V); Yukon Haines Junction, Kluane National Park, 4 miles E of the junction of Kawkawulsh and Dezadeash Rivers; ca. 8 miles WSW of the Junction, 60°45′N, 137°30′W, 610 m, 1 Aug. 1973, Douglas & Douglas 6704* (V). USA, Alaska: Talkeetna Mountains, 62°48'N, 148°01'W, 850 m, 2-Sep-1978, Talbot T8023-V-1915* (DAO); Washington: Jefferson Co.: Buckhorn Mountain, Olympic National Park, T27N R4W S13 SE1/4, 47°49′N, 123°06′W, 2130 m, 8 June 1979, Buckingham 2129*, (OLYM); Royal Basin, Olympic National Park, Ridge between Royal Creek and Dungeness River, 48°08'N, 123°07'W, Aug.-1983, Dalton 2656* (OLYM); ? Co.: Cascade Mts. Vasey s.n.*, (US 556750).

Calamagrostis sesquiflora: CANADA, British Columbia, QCI, 53°10′N, 132°27′W, 24 July 1897, Newcombe 18699 (CAN); Athlow Bay, QCI, 53°38′N, 132°59′W, 122 m, 13 June 1957, Calder & Saville 21456 (DAO); McCliton Cr., QCI, 53°39′N, 132°35′W, 19 June 1957, Calder, Taylor & Saville, 21662 (DAO); Skidegate Channel, QCI, 53°09′N, 132°31′W, 91 m, 25 July 1957, Calder, J. A.; Taylor, R. L.; Saville, D. B. O.,

22928, (DAO); Newton Point, QCI, 53°08'N, 132°30'W, 25 July 1957, Calder, Taylor & Saville 22966 (DAO); Moresby Logging Camp, QCI, 52°55′N, 132°03′W, 29 July 1957, Calder, Taylor & Saville 23126 (DAO); Shields Bay, QCI, 53°21'N, 132°29'W, 731 m, 8 Aug. 1957, Calder & Taylor 23279 (DAO); Jalun Lake, QCI, 53°58'N, 132°52'W, 625 m, 1 July 1964, Calder, J. A.; Taylor, R. L., 35644, (DAO); Long Arm, QCI, 53°12′N, 132°16′W, 305 m, 15 July 1964, Calder & Taylor 35976 (DAO); Kootenay Inlet, QCI, 52°51′N, 132°11′W, 21 July 1964, Calder, J. A.; Taylor, R. L., 36192, (DAO); QCI, 52°56'N, 132°04′W, 570 m, 25 July 1964, Calder & Taylor 36310 (DAO); Sunday Inlet, QCI, 52°39′N, 131°55′W, 2 m, 5 Aug. 1964, Calder & Taylor 36639 (DAO); QCI, 23 July 1910, Spreadborough, 87609, (CAN); Bigsby Inlet, QCI, 52°37′N, 131°45′W, 213 m, 5 July 1957, Calder, Taylor & Saville, 22141* (DAO); Graham Island, QCI, 53°20'N, 132°25'W, 732 m, 8 Aug. 1957, Calder & Taylor 23279* (V); Mt. de la Touche, QCI, 52°42′N, 132°02′W, 610 m, 16 Aug. 1957, Calder & Taylor 23571* (DAO); Mosquito Lake, QCI, 53°04'N, 132°07'W, 701 m, 24 Aug. 1957, Calder & Taylor 23753* (DAO); Vict. Lk, QCI, 52°20'N, 131°28'W, 5 July 1964, Calder & Taylor 35718* (DAO); Cumshewa Inlet, QCI, 52°55'N, 132°06'W, 213 m, 1 Aug. 1964, Calder & Taylor 36507* (DAO); Brooks Peninsula, Vancouver Island, 50°10'N, 127°45'W, 853 m, Jul-1978, Roemer 7884 (V); Brooks Peninsula, Vancouver Island, 50°10′N, 127°45′W, 853 m, Jul-1978, Roemer 7890* (V); Chanal, Port, 53°36'N, 132°54'W, 0 m, Jul-1979, Roemer 79159* (V); Brooks Peninsula, Cassiope Pond, Vancouver Island, 50°10′N, 127°45′W, 640 m, 7 July 1981, Ogilvie, Hebda & Roemer 8173113* (V); Doom Mountain, 50°10′N, 127°46′W, 760 m, 17 Aug. 1981, Ogilvie, Hebda & Roemer 8181711* (V); Cassiope Pond, 50°10′N, 127°45′W, 670 m, 2 Aug. 1981, Ogilvie, Hebda & Roemer 818211 (V); Brooks Peninsula, Doom Mountain, Vancouver Island, 50°10'N, 127°46'W, 730 m, 5 Aug. 1981, Ogilvie, Hebda & Roemer 818546 (V); Brooks Peninsula, Doom Mountain, Vancouver Island, 50°10′N, 127°46′W, 610 m, 7 Aug. 1981, Ogilvie, Hebda & Roemer 818717 (V); Brooks Peninsula, Cladothamnus Lake, Vancouver Island, 50°09'N, 127°45′W, 730 m, 8 Aug. 1981, Ogilvie, Hebda & Roemer 81894* (V); Louise Island, QCI, 52°57'N, 131°38'W, 835 m, 7 Aug. 1997, Lomer & Grove 97239 (V); Graham Island, Mount Raymond, QCI, 53°16'N, 132°13′W, 975 m, 9 July 1997, Lomer & Grove 97243 (V); Graham Island, Mount Stapleton, QCI, 53°15′N, 132°19'W, 880 m, 15 July 1997, Lomer & Grove 97295 (V); Moresby Island, N side of Mount Moresby, QCI, 53°01′N, 132°13′W, 760 m, 15 July 1997, Lomer & Grove 97312 (V); Graham Island, Mount Raymond, QCI, 53°16′N, 132°13′W, 975 m, 16 July 1997, Lomer & Grove 97320 (V); Graham Island; Mount Tian, QCI, 53°48'N, 133°03'W, 487 m, 17 July 1997, Lomer & Grove 97375 (V); Graham Island, QCI, 53°39'N, 132°44′W, 700 m, 17 July 1997, Lonier & Grove 97378 (V); Dinan Creek, QCI, 53°39'N, 132°44'W, 700 m, 17 July 1997, Lomer & Grove 97386* (V); Graham Island, QCI, 53°34'N, 132°43'W, 715 m, 16 July 1997, Lomer & Grove 97394 (V); Apex Mountain, QCI, 52°42'N, 131°53'W, 914 m, 19 Aug. 1997, Lomer & Grove 97448* (V); Graham Island, Mount LaPerouse, QCI, 53°14′N, 132°30′W, 1066 m, 20 Aug. 1997, Lonier & Grove 97494 (V); Moresby Island, Mosquito Mountain, QCI, 53°01′N, 132°09′W, 792 m, 20 Aug. 1997, Lomer &

Grove 97498* (V); Anna Lake, 50°30'N, 125°18'W, 25 Aug. 1992, Ogilvie s.n. (V); Mount Laysen, QCI, 52°41′N, 131°51′W, 950 m, 20 Aug. 1992, Ogilvie s.n. (V); Mount Laysen, QCI, 52°41'N, 131°51'W, 950 m, 20 Aug. 1992, Ogilvie s.n. (V); Moresby Island, Takakia Lake, QCI, 52°56'N, 132°04'W, 17 Aug. 1980, Ogilvie s.n. (V); Takakia Lake, QCI, 52°55'N, 132°03'W, 823 m, 19 Aug. 1980, Ogilvie, Roemer & Mersereau s.n. (V); USA, Alaska: Aleutians West Co.: Aleutian Islands: Akutan, 800 ft, 12 Aug. 1934, L. Norberg, 610, (MO); RUSSIA: Kuril Archipelago: Makanrushi, inland from Zakat Bay, 49°44′16″N 154°24′52″E, 100 ft., 18 Aug. 1997, Sarah Gage SG4611* (WTU); Shumshu, about 2 km south of Pochtareva Cape, 50°49'07"N 156°29'31"E, 50 feet, 8 Aug. 1997, Sarah Gage SG4212* (WTU); Paramushir, inland from Severo-Kurlisk by road, along eastern edge of Ebeko Volcano, 50°40′52″N 156°04′52″E, 1200 feet, 5 Aug. 1997, Birgit Semsrott BS1178* (WTU); Ushishir Group, Yanchika Island, inland environs of Kraternaya Bay, 47°30′33″N 152°49'05"E, 1 Aug. 1997, Sarah Gage SG4054* (WTU): inland environs of Kraternava Bay. 47°31′10″N 152°49′08″E, 1 Aug. 1997, Birgit Semsrott BS1087* (WTU); Kamchatka: Ust-Bolsheretskiy district, village of Ozernovskiy, A. E. Kogevnikov s.n.* 1978 (V113790).

Calamagrostis tacomensis: USA:Washington: Grays Harbor Co.: Mt. Colonel Bob, Olympic Mts., 9 July 1931, Thompson, 7330 (WTU); Jefferson Co.: Marmot Lake, 4000 ft, 23 Aug. 1935, Dickinson 103 (OLYM); Marmot Lake, Olympic Mtns., 4000 ft, 23 Aug. 1935, Dickinson 103 (WTU); McGravey Lake area, 15 Aug. 1990, A. Comulada and P. Maurides (OLYM); Mt. Olympus, 4000 ft., Aug.-07, Flett 3075 (WTU); above Lake Constance, Olympic Mts., 6000 ft, 11 Aug. 1931, Thompson 7869 (MO,US,WTU); Olympic mountains, 5000 ft, Aug. 1895, C.V. Piper s.n. (US); King Co.: Guy Peak, Cascade Mts., 3500 ft., 7 Aug. 1933, Thompson 9686 (WTU); Guy Peak, Snoqualmie Pass, 3500 ft, 7 Aug. 1933, Thompson 9686 (MO); Guy Peak, Snoqualmie Pass, 4000 ft 7 Aug. 1933 Thompson, 9686*, (GH); Kittitas Co.: Beverly, 14 July 1977, Creso 7-50 (Luth); head of Beverly Creek, Wenatchee Mtns., 2 Sept. 1933 Thompson 10044*, (WTU); north fork of the Teanaway River, end of road, below Esmareldi Peaks, 4,500 ft., 21 July 1963, Maas 1209* (WTU); Lewis Co.: Goat Rocks

Primitive Area, 7000 ft, 6 Aug. 1940, Thompson 15198 (MO); Mason Co.: Mt. Washington, 4500 ft, 11 Aug. 1985, Maxwell 835 (Olym); Pierce Co.: Tipsoo Lake, Mount Rainier, 12 Sept. 1932, Warren 1547 (WTU); Goat Mountains, 5 Aug. 1895, Allen 177 (MO); Mt. Tacoma, 23 Aug. 01, Flett, 1959 (WTU); Paradise Valley, Mt. Rainier, 5600 ft, 23 Aug. 1901, Flett 1959 (NY); Paradise Lake, Mt. Rainier, 26 July 1931, Thompson 7635 (WTU); Mount Tacoma, 25 Aug. 1901, Flett 2076 (WTU); Alpine slopes on Governor Ridge, Mt. Rainier NP, 6000 ft, 27 Aug. 1931, Thompson 8097 (US); Goat Pass, Mt. Rainier, 5500 ft. 26 July 1934, Thompson 11079 (MO,WTU); Mount Rainier NP, nr. Klapatche Park, 3 Sept. 1975, Creso & Leraas 5-19740 (Luth); Mt. Rainier, 6-7000 ft, Aug. 1895, Piper s.n., (US); Silver Falls, Ohanapecosh, Mt. Rainier, 2200 ft, 31 July 19, Flett s.n. (US); west of Reflection Lake, Mt. Rainier, 17 July 19, Flett s.n, (US); Mount Rainier NP, along trail from Tipsoo L. to Dewey L., 13-Sep-1975, Creso & Beck 5-858 (Luth); Mt. Wow, Rainier National Park, 5000 ft, 15 Aug. 1935, Thompson 12593 (MO, WTU); Mt. Rainier, near Greenwater R., 15-Sep-1945, Schallert 19582 (MO); Chinook Pass, Mt. Rainier National Park, 17 Aug. 1935 (WTU); Paradise Valley, Parks & Parks 21045 (MO); Goat Mountains, 5 Aug. 1895, Allen 177* (GH); Alpine slopes above Owyhigh Lakes, Mt. Rainier National Park, 5500 ft., 27 Aug. 1931, Thompson 8097 (WTU); Mount Rainier NP, summit of Ipsut Pass, 28 July 1951, M.C. Huntley s.n. (Luth.); Mt. Rainier, Chinook Pass, 1900 m, 17 Aug. 1935, Eyerdam s.n. (MO); Skamania Co.: high mountains, 11 Aug. 1886, Suksdorf 201 (US); 11 Aug. 1886, Suksdorf, 909, (MO, NY); high mountains, 27 Aug. 1890, Suksdorf 1025 (MO,US); Pumice Plain north of crater breach, Mount St. Helens, 4 Aug. 1994, Titus s.n. (WTU); Camp 19, 4 Aug. 1899, Flett 1390 (WTU); 27 Aug. 1890, Suksdorf s.n. (US); Columbia National Forest. Along Wind R., 1600 ft, 20 May 1926, Ingram 2022* (OSU); Snohomish Co.: Perry Creek, 25 July 1983, Hagen s.n. (WTU); Yakima Co.: Chinook Pass, Cascade Mtns., 5500 ft., 1 Aug. 1940, Thompson 15149 (WTU); Oregon: Harney Co.: Steens Mts. Region 11.5 mi E and 10 mi due S of Frenchglen, T33S R32 3/4E sec 26, 6200 ft, 25 July 1954, Hansen 893* (OSU); Steens Mountains, 7120 ft, 5 Aug. 1992, Mansfield 92-19449* (OSU).